

Phylogenetic Relationships of Aulacocyclinae (Coleoptera, Passalidae) Inferred from Morphological Characters

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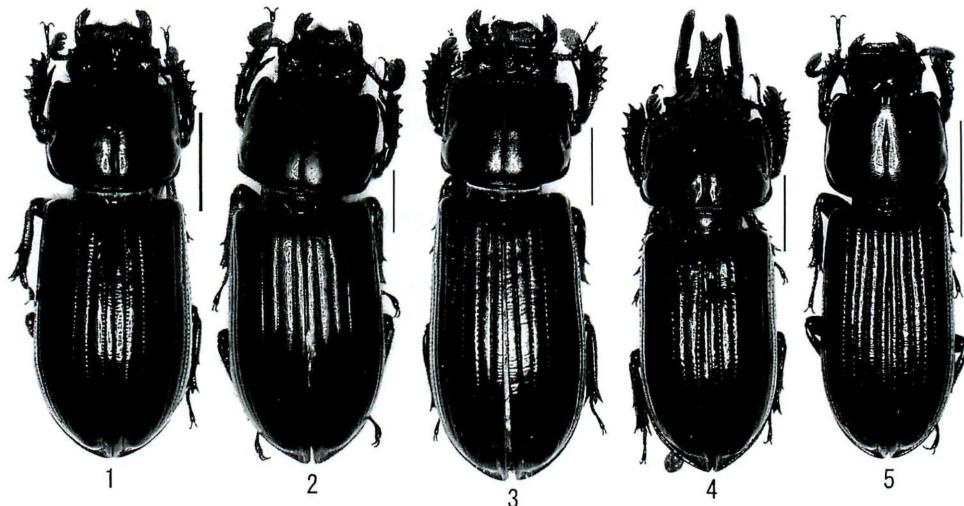
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Abstract Phylogenetic relationships among the five genera of the passalid subfamily Aulacocyclinae, *Aulacocyclus*, *Ceracupes*, *Comacupes*, *Cylindrocaulus* and *Taeniocerus*, are analyzed by the maximum parsimony method using 35 morphological characters. Twenty species of Aulacocyclinae are included in the analysis, with five representative species from five tribes of the Passalinae used as outgroup. The resultant tree indicated monophyly of the subfamily Aulacocyclinae and that of the tribe Aulacocyclini consisting of *Aulacocyclus*, *Comacupes* and *Taeniocerus*. Congeneric species cluster on the same branch with a high bootstrap value for the genera *Cylindrocaulus*, *Ceracupes* and *Comacupes*, whereas species of the genera *Aulacocyclus* and *Taeniocerus* are not separated from each other and no well-defined cluster is recognized for them.

Introduction

The passalid subfamily Aulacocyclinae (Coleoptera, Passalidae) include nearly 50 species distributed in the Palaearctic, Oriental and Australian Regions (HINCKS & DIBB, 1935, 1958; OKANO, 1988; BOUCHER, 1998; BOUCHER & REYES-CASTILLO, 1996, 1997). BOUCHER (2005) divided this subfamily into two tribes: Aulacocyclini consisting of *Aulacocyclus*, *Comacupes* and *Taeniocerus*, and Ceracupini consisting of *Ceracupes* and *Cylindrocaulus* (Figs. 1–5). Furthermore, BOUCHER (2005) studied the phylogenetic relationships among all seven tribes of Passalidae using Trogidae, Lucanidae and Chironidae as outgroups, and suggested monophyly for the family Passalidae, the subfamily Aulacocyclinae consisting of the tribes Aulacocyclini and Ceracupini, and the subfamily Passalinae consisting of the tribes Passalini, Proculini, Solenocyclini,



Figs. 1-5. Habitus of representative species of Aulacocyclinae. Scales, 5 mm. — 1, *Aulacocylus rouxi*; 2, *Comacupes basalis*; 3, *Taeniocerus bicanthatus*; 4, *Ceracupes arrowi*; 5, *Cylindrocaulus davidi*.

Leptaulacini and Macrolinini. However, the phylogenetic relationships among the genera and species of Aulacocyclinae have not yet been elucidated to date. We therefore estimate the phylogenetic relationships among all the five genera of the Aulacocyclinae using the maximum parsimony method based on morphological characters.

Materials and Methods

The phylogenetic relationships of 20 species belonging to all the five genera of the subfamily Aulacocyclinae were estimated by the maximum parsimony method. Five species of the subfamily Passalinae, each of which is a representative of the five tribes of this subfamily, were included in the analysis as outgroup. Species analyzed are listed in Table 1. We used 35 morphological characters to analyze the species in the present study.

The characters and character states, which were adopted from the terminology of GRAVELY (1914) for the external morphological characters, that of REYES-CASTILLO (1970) for the wing vein, and that of LINDROTH (1957) for the male genitalia, were as follows:

Head

1. Upper surface of head: (0) punctate; (1) impunctate.
2. Outer tubercle: (0) present; (1) absent.
3. Inner tubercle: (0) present; (1) absent.
4. Central tubercle: (0) moderately developed, not overhanging; (1) absent; (2)

Table 1. List of the species studied for the analysis.

Species	Collection locality and date
Subfamily Aulacocyclinae	
Tribe Aulacocyclini	
<i>Aulacocylus perlatus</i> KAUP	Oro, Papua New Guinea, 5-II-1995
<i>A. rouxi</i> HELLER	Reviere Blueu, New Caledonia, 27-XII-1997
<i>A. tricuspidis</i> KAUP	Mont Koghis, New Caledonia, 25-XII-1997
<i>Comacupes basalis</i> (SMITH)	Mt. Apo, Mindanao, 15-I-1984
<i>Co. cavicornis</i> (KAUP)	Penag, Malay Peninsula, 17-XII-1992
<i>Co. cylindraceus</i> (PERTY)*	Trus Madi, Sabah, 25-IV-1992
<i>Co. foveicollis</i> KUWERT	Trus Madi, Sabah, 20-IV-1999
<i>Co. masoni</i> STLICZKA	Kota Tinggi, Malay Peninsula, 21-III-1996
<i>Co. stoliczkae</i> GRAVELY	Brumas, Sabah, 24-VIII-1985
<i>Taeniocerus bicanthatus</i> (PERCHERON)*	Bareo, Sarawak, 11-I-1990
<i>T. mourzinei</i> BOUCHER	Putao, Myanmar, 20-VI-1998
<i>T. platypus</i> KAUP	Trus Madi, Sabah, 25-IV-1992
<i>T. pygmaeus</i> (KAUP)	Langkawi, Malay Peninsula, 24-VIII-2003
Tribe Ceracupini	
<i>Ceracupes arrowi</i> HELLER	Nanshanchi, Formosa, 23-VIII-1986
<i>Ce. chingkini</i> OKANO	Chiang Rai, Thailand, 6-VIII-1987
<i>Ce. fronticornis</i> (WESTWOOD)*	Chiang Mai, Thailand, 31-XII-1992
<i>Ce. yui</i> OKANO	Wushe, Formosa, IV-1964
<i>Cylindrocaulus bucerus</i> FAIRMAIRE*	Sichuan, China, 9-VI-1997
<i>Cy. davidi</i> BOUCHER et REYES-CATILLO	Dalianshan, Sichuan, China, 14-V-1996
<i>Cy. patalis</i> (LEWIS)	Ishizuchi, Ehime, Japan, 28-VII-1997
Subfamily Passalinae	
Tribe Solenocyclini	
<i>Pentalobus palinii</i> (PERCHERON)	San Pedro, Ivory Coast, VIII-2000
Tribe Leptaulacini	
<i>Leptaulax dentatus</i> (FABRICIUS)*	Phu Pan, Laos, 3-III-2003
Tribe Macrolinini	
<i>Macrolinus latipennis</i> (PERCHERON)*	Tapah, Malay Peninsula, 24-III-1997
Tribe Proculini	
<i>Proculus mniszechi</i> KAUP	Purulha, Guatemala, 14-IX-2001
Tribe Passalini	
<i>Passalus punctiger</i> St. FARGEAU et SERVILLE	San Marcos, Guatemala, 26-IX-2001

*: The type species of the genus.

developed, overhanging in the anterior portion; (3) extremely produced forwards.

5. Frontal ridge: (0) present; (1) absent.
6. Supraorbital tubercle: (0) absent; (1) present.
7. Supraoccipital ridge: (0) present; (1) absent.
8. Upper tooth of mandible: (0) moderately developed; (1) absent; (2) extremely produced forwards and upwards.
9. Middle lower tooth of mandible: (0) mobile; (1) immobile.
10. No. of pubescent antennal lamellae: (0) 4 or more; (1) 3.
11. Concave hairless area on the anterior margin of labrum: (0) absent; (1) present.
12. No. of lacinial spines: (0) single; (1) double.
13. Distal lacinial spine: (0) not cleft; (1) cleft.
14. Scars on mentum: (0) present; (1) absent.
15. Median ridge on mentum: (0) absent; (1) present.
16. Distinct pentagonal smooth area on the central portion of mentum: (0) absent; (1) present.

Thorax

17. Marginal groove of pronotum: (0) incomplete, absent on the anterior margin; (1) almost complete except at the middle of anterior margin.
18. Median sulcus of pronotum: (0) incomplete; (1) complete.
19. Tubercles on anterior margin of pronotum: (0) absent; (1) present.
20. Scars of pronotum (punctures): (0) punctate; (1) impunctate.
21. Scars of pronotum (hairs): (0) hairless; (1) hairy.
22. Procoxae: (0) not covering the middle portion of prosternum at all; (1) incompletely covering it; (2) completely covering it.
23. Scutellum: (0) punctate; (1) impunctate.
24. Scars on mesosternum: (0) present; (1) absent.
25. Mesosternum: (0) impunctate; (1) partially punctate; (2) entirely punctate.
26. Metasternum: (0) punctate; (1) impunctate.
27. Elytral dorsal striae: (0) impunctate; (1) finely punctate; (2) strongly punctate.
28. Elytral lateral striae: (0) strongly punctate; (1) finely punctate.
29. Elytral lateral interstriae: (0) impunctate and hairless; (1) punctate and hairy.
30. Wing vein 2A₂ (one of the branches of the second anal vein) of hind wing: (0) absent; (1) present.
31. No. of teeth on the outer margin of mesotibia: (0) 0; (1) 1; (2) 2 or more.

Abdomen

32. No. of visible abdominal sternites: (0) 6; (1) 5.
33. Abdominal sternites: (0) impunctate; (1) punctate only in anterior sternites; (2) wholly punctate.

Table 2. Character state matrix for 20 species of Aulacocyclinae and 5 species of Passalinae. See text for coding.

Species	Characters																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>Aulacocyclus perlatus</i>	1	1	2	1	0	1	1	0	1	0	1	1	0	1	0	2	1	0	1	0	0	1	1	0	1	1	0	1	1	0	1	1	0	1	1
<i>A. rouxi</i>	1	1	1	2	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>A. tricuspis</i>	1	1	1	2	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
<i>Comacupes basalis</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	0	1	2	0	1	1	1	1	1	1	1	1	1	1	1	2	1	1
<i>Co. cayicornis</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	2	1
<i>Co. cylindraceus</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	1	0	2	0	1	2	0	1	1	1	1	1	1	1	1	1	1	1
<i>Co. foveicollis</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	2	0	1	1	0	2	0	0	1	1	1	1	1	0	1	1
<i>Co. masoni</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	1	0	2	0	1	2	0	1	1	1	1	1	1	1	1	1	1	1
<i>Co. stoltezkae</i>	0	1	1	2	1	0	1	1	0	1	0	1	0	1	0	1	0	1	0	2	0	1	2	0	1	1	1	1	1	1	1	1	1	2	1
<i>Taeniocerus bicanthatus</i>	0	1	1	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	2	0	1	1	0	2	0	0	1	1	1	1	1	0	1	1
<i>T. mourzinei</i>	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	2	1	1	0	0	1	0	0	1	1	1	1	0	1	1
<i>T. platypus</i>	1	1	1	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	2	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1
<i>T. pygmaeus</i>	1	1	1	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	2	1	1	0	1	0	1	0	1	1	1	1	1	0	1	1
<i>Ceracipes arrowi</i>	1	1	1	3	1	0	1	2	0	1	1	1	0	0	1	1	0	0	0	2	1	1	0	2	0	0	1	2	1	0	1	1	1	1	1
<i>Ce. chingkini</i>	1	1	1	3	1	0	1	2	0	1	1	1	0	0	1	1	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	1	0	1	1
<i>Ce. fronticornis</i>	1	1	1	3	1	0	1	2	0	1	1	1	0	0	1	1	0	0	0	2	1	1	0	0	2	0	0	1	2	1	0	0	1	0	1
<i>Ce. yui</i>	1	1	1	3	1	0	1	2	0	1	1	1	0	0	1	1	0	0	0	2	1	1	0	2	0	0	1	2	1	0	0	1	0	1	1
<i>Cylindrocaulus bucerus</i>	1	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cy. davidi</i>	1	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cy. patalis</i>	1	1	1	1	1	0	1	1	0	1	0	1	1	0	1	1	0	0	1	1	1	0	1	1	2	0	0	1	2	1	0	0	1	0	1
<i>Pentalobus patinii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptanulax dentatus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Macrolinus latipennis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proculus mniszechii</i>	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Passalus punctiger</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Male genitalia

34. Basal piece and parameres of male genitalia: (0) separated; (1) united.

Body

35. Body thickness divided by elytral width at the widest point: (0) less than 0.7; (1) 0.7 or more.

Eight of the above characters (2, 9, 10, 17, 22, 30, 32, 35) were also used by BOUCHER (2005).

The character state matrix is shown in Table 2. Character 30 was considered inapplicable for the three species, *Cylindrocaulus bucerus*, *Cy. patalis* and *Proculus mniszechi*, all of which have the hind wings atrophied. The character was coded as “—” for these species. All characters were equally weighted and set as unordered. Analysis was performed using the Branch and Bound algorithm of PAUP (version 4.0; SWOFFORD, 2002) to find the most parsimonious networks rooted with outgroup. The strict consensus tree was then obtained from the shortest trees, and the three indices, consistency index excluding uninformative characters, retention index and rescaled consistency index, were calculated for goodness-of-fit statistics. Bootstrap analysis with heuristic search was performed for the trees with 1,000 replicates.

Results and Discussion

There was no uninformative character among the 35 characters used in the present study. One thousand forty equally parsimonious trees (tree length = 84, consistency index = 0.524, retention index = 0.791, rescaled consistency index = 0.414) were detected and the strict consensus tree was obtained for these shortest trees (Fig. 6).

Monophyly of the subfamily Aulacocyclinae was supported by the present results with a bootstrap value of 80%. Species of Aulacocyclinae shared the following character states (which were not shared by the outgroup species): 1) the inner tubercles absent; 2) the supraoccipital ridge absent; 3) the marginal groove of the pronotum almost complete; 4) the abdomen with five visible sternites; 5) the hind wing with the vein 2A₂ (except for *Cylindrocaulus patalis* and *Cy. bucerus* in which the hind wing is atrophied). Of these, the presence of the hind wing vein 2A₂ was also indicated by BOUCHER (2005). Three major lineages were recognized in the subfamily Aulacocyclinae; the first one corresponded to the genus *Cylindrocaulus* (bootstrap value, 80%), the second to the genus *Ceracupes* (bootstrap value, 62%), and the third to the tribe Aulacocyclini consisting of the remaining three genera (bootstrap value, 56%). Further, in Aulacocyclini, species of the genus *Comacupes* formed a monophyletic group with a bootstrap value of 70%. However, monophyly of the tribe Ceracupini consisting of *Ceracupes* and *Cylindrocaulus* was not ascertained by the present analysis, the genera *Ceracupes* and *Cylindrocaulus* formed a monophyletic group only in 320 trees (30.8%) of the shortest 1,040 trees. In none of the shortest trees, species of *Aulacocyclus* or

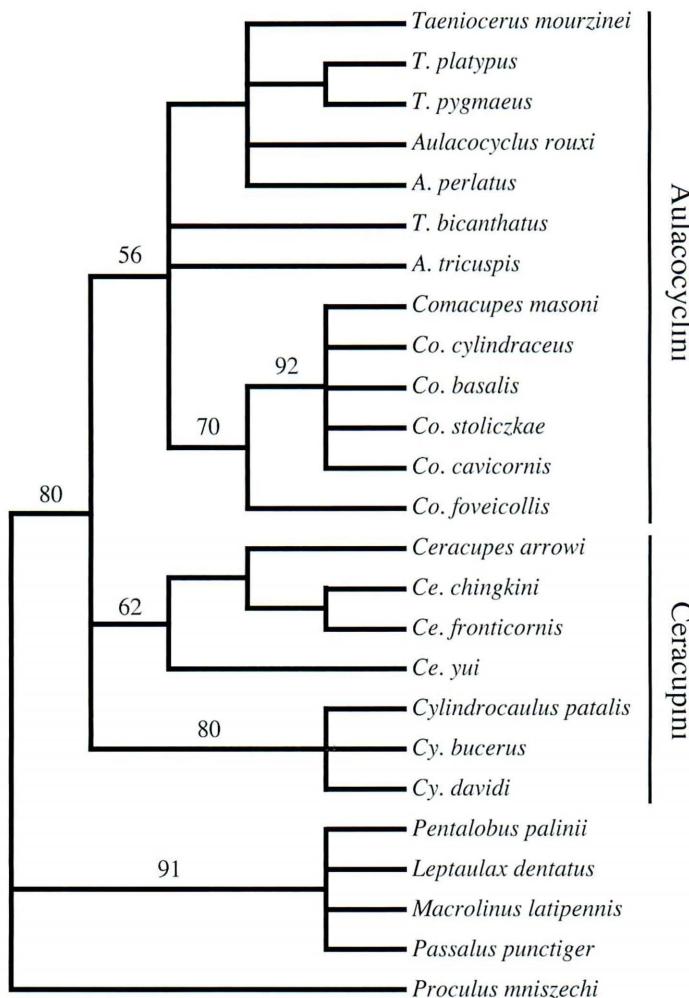


Fig. 6. Strict consensus tree of the shortest 1,040 trees. Bootstrap values (>50%; 1,000 replications) were shown above each branch.

Taeniocerus formed a monophyletic group. Species of the genera *Aulacocyclus* and *Taeniocerus* were not separated from each other, and no well-defined cluster was recognized among them.

The derived character states characterizing the species of each monophyletic genus were as follows: *Cylindrocaulus*, 1) the upper tooth of mandible absent, 2) the head with supraorbital tubercles, 3) the pronotum with tubercles on the anterior margin, 4) the procoxae incompletely covering the middle portion of prosternum; *Ceracupes*, 1) the upper tooth of mandible extremely produced, 2) the labrum with a concave hairless area on the distal end; *Comacupes*, 1) the mentum with a median ridge. Further, the species

of the tribe Aulacocyclini share the character state, the middle lower tooth immobile, whereas both the species of the genera *Cylindrocaulus* and *Ceracupes* and the outgroup species of Passalinae have the middle lower tooth mobile.

In the present study, almost all known Aulacocyclinae species belonging to the Palaearctic or Oriental genera *Cylindrocaulus*, *Ceracupes*, *Comacupes* and *Taeniocerus* were examined (though we were not able to examine *Comacupes intermedius* HINCKS and *Taeniocerus bicuspis* (KAUP)), whereas only three species of *Aulacocylus* were examined though this genus includes 20 or more known species mainly from the Australian Region (HINCKS & DIBB, 1935; 1958; BOUCHER & REYES-CASTILLO, 1997). In order to better estimate the phylogenetic relationships among the genera of Aulacocyclini, more characters need to be examined.

In the resultant tree of the present study, the phylogenetic relationships among *Cylindrocaulus*, *Ceracupes* and Aulacocyclini were not resolved. Moreover, the relationships among the species in the genera *Aulacocylus* and *Taeniocerus* were also not clearly resolved. Further studies using new characters are therefore required in order to elucidate the phylogeny of the subfamily Aulacocyclinae. Molecular phylogenetic analyses are expected to improve the resolution of phylogeny.

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要 約

細谷忠嗣・荒谷邦雄・近 雅博: 形態形質にもとづき推定されたツツクロツヤムシ亜科の系統関係。——ツツクロツヤムシ亜科の5属, *Aulacocylus*, *Ceracupes*, *Comacupes*, *Cylindrocaulus* と *Taeniocerus* の系統関係を35形態形質にもとづき最節約法によって解析した。ツツクロツヤムシ亜科の20種と、クロツヤムシ亜科の5族を代表する5種を外群として分析に含めた。解析の結果、ツツクロツヤムシ亜科とツツクロツヤムシ族 (*Aulacocylus*, *Comacupes* および *Taeniocerus* からなる) の単系統性が支持された。さらに、*Cylindrocaulus*, *Ceracupes* と *Comacupes* の3属の種は、それぞれ同じ枝にまとまり、高いブートストラップ値で支持された。一方、*Aulacocylus* と *Taeniocerus* の2属の種は分離されず、またそれらの種について明確なクラスターは認識されなかった。

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Spectrophotometric Analysis of Dorsal Coloration in *Phelotrupes auratus* (Coleoptera, Geotrupidae): A Comparison of Beetles Collected in 2001 and 2005

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The coprophagous beetle, *Phelotrupes auratus* (MOTSCHULSKY) (Coleoptera, Geotrupidae), is known to exhibit considerable variation in color (MIZUNO, 1964). TSUKAMOTO (1994) introduced a possibility that the coloration of this species may have changed over time in the Nara City population. However, based on qualitative assessments of dorsal coloration by eye, MIZUTA (2000) reported that there were no significant differences in beetles collected from Nara City in 1972–1975 and 1996–1997.

On the other hand, WATANABE *et al.* (2002) conducted spectrophotometric analyses of the dorsal coloration in *Phelotrupes auratus*, and found that the wavelength of the highest peak in the reflectance spectrum of visible region (400–700 nm), which they named $\lambda_{\text{max}}(\alpha)$, was the optimal parameter for discriminating the coloration of this species.